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Spermophilus variegatus.

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Spermophilus variegatus (Erxleben, 1777)

Rock Squirrel

Sciurus variegatus Erxleben, 1777:421. Type locality restricted to "Valley of Mexico, near the City of Mexico" by Nelson (1898:898).

Sciurus grammurus Say, in James, 1823:72. Type locality Purgatory River, near mouth of Chacuaco Creek, Las Animas Co., Colorado.

Sciurus buccatus Lichtenstein, 1830:117. Type locality unknown.

Sciurus macrourus Bennett, 1833:41. Type locality western Mexico.

Spermophilus couchii Baird, 1855:332. Type locality Santa Caterina, a few miles W Monterrey, Nuevo Leon.

Spermophilus buckleyi Slack, 1861:314. Type locality Packsaddle Mountain, Llano Co., Texas.

Spermophilus variegatus Nelson, 1898:898. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Subfamily Sciurinae, Genus *Spermophilus*, Subgenus *Otospermophilus*. The genus *Spermophilus* contains 36 species distributed as follows: 12 Palearctic, 23 Nearctic, and 1 Holarctic (Honacki et al., 1982). There are eight subgenera of *Spermophilus*, two Palearctic, five Nearctic, and one Holarctic. *Spermophilus variegatus* is one of five species in the subgenus *Otospermophilus*; the others are *S. adocetus*, tropical ground squirrel; *S. annulatus*, ringtailed ground squirrel; *S. atricapillus*, Baja California ground squirrel; and *S. beecheyi*, California ground squirrel (Hall, 1981). There are eight subspecies of *S. variegatus* as follows:

S. v. buckleyi Slack, 1861:314, see above.

S. v. couchii Baird, 1855:332, see above.

S. v. grammurus (Say in James, 1823:72), see above (*juglans* Bailey a synonym).

S. v. robustus (Durrant and Hansen, 1954:264). Type locality Pass Creek, Deep Creek Mountains, 8,000 ft, Juab Co., Utah.

S. v. rupestris (J. A. Allen, 1903:595). Type locality Rio Sestin, northwestern Durango.

S. v. tularosae (Benson, 1932:336). Type locality French's Ranch, 5,400 ft, 12 mi NW Carrizozo, Lincoln Co., New Mexico.

S. v. utah (Merriam, 1903:77). Type locality foot Wasatch Mountains, near Ogden, Weber Co., Utah.

S. v. variegatus (Erxleben, 1777:421), see above (*buccatus* Lichtenstein and *macrourus* Bennett are synonyms).

DIAGNOSIS. The rock squirrel is a member of the subgenus *Otospermophilus*, whose diagnostic characters include: pelage with a variegated pattern of black, white, and buff; infraorbital foramen oval with masseteric tubercle nearly ventral to foramen; width of cranium at postorbital constriction slightly greater than least interorbital breadth; fossae anterolateral to incisive foramina deep; upper cheekteeth brachyodont, M1 and M2 subquadrate in occlusal outline; metaloph of P4, M1, and M2 separated from protocone by sulcus; M3 slightly larger than M2; metaloph of M3 absent; protolophid of p4 absent and protoconid slightly larger than hypoconid; cheek pouches large; baculum with proximal end enlarged into a knob; and atlantoscapularis dorsalis muscle present (Hall, 1981).

Spermophilus variegatus (Fig. 1) is the largest member of the subgenus *Otospermophilus* and the largest ground squirrel within its geographic range. The presence of a supraorbital foramen and grayish (or mixed black and white) sides of the head in *S. variegatus*, *S. beecheyi*, and *S. atricapillus* distinguishes these three species from *S. annulatus* and *S. adocetus*, in which the supraorbital foramen is closed and the sides of the head are tawny or buffy. *S. beecheyi* and *S. atricapillus* are characterized by whitish sides of the neck and shoulders, separated by a dark dorsal triangle, whereas *S. variegatus* lacks the whitish shoulders. *S. variegatus* is separated geographically from *S. atricapillus*, which is confined to Baja California, and from *S. beecheyi*, which, in Nevada and California, occurs west of the range of *S. variegatus* (Hall, 1981). Except for its larger size, the skull of *S. variegatus* is indistinguishable from that of *S. beecheyi* (Hall, 1981). Externally, these two ground squirrels differ in size, pelage and in relative tail length, which is greater in *S. variegatus*. In *S. variegatus* tail length is 73 to 82% of body length and usually more than 44% of total length; in *S. beecheyi*, tail length is 62 to 77% of body length and usually less than 44% of total length (Blair et al., 1968).

GENERAL CHARACTERS. In external features the rock squirrel is not modified strongly for fossorial life as are many other ground squirrels (subgenera *Xerospermophilus*, *Ictidomys*, *Spermophilus*) and their close relatives the prairie dogs (*Cynomys* sp.). Rather, *S. variegatus* more closely resembles typical tree squirrels of the genus *Sciurus* than typical ground squirrels. The head and eyes of the rock squirrel are large, and the ears extend above the top of the head and are much longer than wide. The neck is moderately long for a squirrel but stout, and the limbs are of medium length in comparison with those of other squirrels, with the forelimbs shorter than the hind limbs. The tail is long and bushy, though less so than in typical tree squirrels. Long claws are borne on all digits except the pollex, which is extremely short and carries a broad nail. Digits of the manus, ranked in order from shortest to longest, are: 1, 5, 2, 4, 3, a pattern similar to that of other ground squirrels and in contrast to that of more arboreal squirrels, in which the fourth digit is longer than the third. All five digits of the pes are long, but their relative lengths are the same as those of the manus (Bryant, 1945).

Ranges of means of standard external and selected cranial measurements (in mm) and ranges of original measurements (in parentheses) for the seven subspecies of *S. variegatus* (Howell, 1938) are as follows: total length, 466 to 503 (430 to 540); tail vertebrae, 189 to 233 (174 to 263); hind foot, 57 to 62.7 (53 to 65); and ear from notch (dry), 17 to 26.3 (15 to 29); greatest length of skull, 57.9 to 65.6 (56 to 67.7); palatilar length, 27.7 to 31.5 (26 to 32.5); zygomatic breadth, 35.6 to 40.5 (34 to 42.4); cranial breadth, 24.1 to 26.1 (23.5 to 26.6); interorbital breadth, 13.5 to 16.9 (13.2 to 18.8); postorbital constriction, 16.9 to 17.9 (16 to 19.6); length of nasals, 20.4 to 23.8 (18.5 to 24.8), and length of maxillary tooth row, 11.3 to 13.4 (10.7 to 14). Howell (1938) reported separate means for samples of adult males and females for

FIG. 1. Photograph of a rock squirrel. Photograph from a slide by J. G. Hall.

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the left mandible of *Spermophilus variegatus grammurus* (USNM 168267, adult female from 18 mi S La Junta, Otero Co., Colorado; occipitonasal length 58.0 mm). Photographs by DFS.

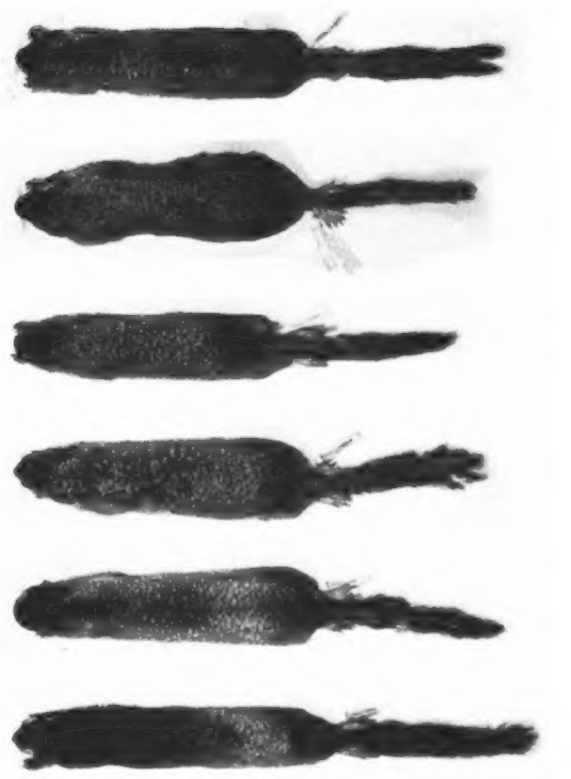

FIG. 3. Skins of *Spermophilus variegatus* illustrating range of variation in color pattern. From bottom to top, *S. v. buckleyi* (USNM 97155 female from Llano, Llano Co., Texas), *S. v. couchii* (USNM 116939 male from Saltillo, Coahuila, Mexico), *S. v. grammurus* (USNM 128541 female from Capitan Mts, Lincoln Co., New Mexico), *S. v. rupestris* (USNM 51282 male from Chihuahua Mts, Chihuahua, Mexico), *S. v. utah* (USNM 264248 female from 3 mi S Mantua, Box Elder Co., Utah), *S. v. variegatus* (USNM 34924 male from Acambaro, Michoacan, Mexico). Photographs by DFS.

three subspecies (*variegatus*, *rupestris*, and *utah*) but performed no statistical comparisons between the sexes; however, in the most instances (25 of 28), means for males were larger than those for females, suggesting sexual dimorphism for size in the rock squirrel. Published data on body mass also indicate that males average larger than females. Reported mean weights (in g) of adult rock squirrels from Coahuila, Mexico (Baker, 1956) are: 4 males, 621 (range 470 to 875), 5 nonpregnant females, 546 (450 to 634); from central Texas (Johnson, 1979): 13 males, 855.4, 19 females, 734.5; from Nevada (Hall, 1946): 5 males, 684.3 (580.3 to 742.5), 3 nonpregnant females, 708.6 (643.5 to 795.5). Adult rock squirrels show substantial seasonal weight gains during preparation for hibernation (Juelson, 1970; Layton, 1973).

The skull of *S. variegatus* (Fig. 2) has a moderately convex dorsal profile, an ovate shallow braincase, and a broad interorbital region (Bryant, 1945). The parietal ridges meet near the posterior end of the cranium to form a slight crest; the rostrum is short and broad, tapering gradually; postorbital processes are long, stout and decurved, and the supraorbital borders of the frontals are slightly elevated and notched anteriorly (Howell, 1938). The infraorbital canal and foramen are narrowly oval to subtriangular with masseteric tubercle prominent at the ventrolateral margin of the foramen (Bryant, 1945; Hall, 1981). The auditory bullae are globular in shape but somewhat compressed laterally; the auditory meatal tubes are short (Howell, 1938). The body of the lower jaw is long and not deep; the diastemal part of the mandible is long and slender; the alveolar border of the mandibular body is level with the level of the anterior tip of the mandible; the coronoid process is long, narrow, and projects posteriad; and the angular process is large, extends posteriad as far as the condyloid process, and is ridged along its posterior edge (Bryant, 1945).

The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Upper incisors are stout and only moderately recurved; lower incisors are longer, more slender, and less curved than the upper incisors, and the lowers project forward at a moderate angle (Bryant, 1945). The anterior upper premolar (P3) is simple, peglike, and less than one-quarter the size of P4, which is molariform (Hall, 1981). Molars are subquadrate; m3 is much elongated posteriorly (Bryant, 1945). Parastylar ridges on M1 and M2 arise evenly from the protocones without abrupt change in direction (Hall, 1981). Cusps on cheek teeth are connected by crests of moderate height.

The pattern of the dorsal pelage tends to be variegated black and white, often with buff, especially over the rump. The dorsum is crossed by many indistinct wavy markings of brown and black, averaging 5 mm in width (Dalquest, 1953). Pelage coloration in rock squirrels is highly variable both within and between populations. The head varies from pinkish buff or pinkish cinnamon to seal brown and fuscous black; the back varies from grayish white mixed with cinnamon buff to snuff brown, mikado brown, bone brown, and dark blackish brown; and the tail is mixed black or brown and buffy white (Howell, 1938). In some races, the head, foreback, or entire dorsum is black (Fig. 3), although there can be considerable variation in the amount of melanin within subspecies (Baker, 1960). Color of underparts is variable, generally grayish white, buffy white, or pinkish buff to cinnamon buff (Howell, 1938).

DISTRIBUTION. In the United States, the rock squirrel occurs from the Edwards Plateau and Trans-Pecos Texas westward through much of New Mexico, Arizona, and into southeasternmost

California; northward into Colorado (primarily west of the Front Range), most of Utah, and eastern Nevada. Its range encompasses much of Mexico from Puebla, Colima, Guerrero, Mexico, and Morelos northward to the United States, although it is absent from the eastern coastal lowlands (Fig. 4). Because of its extensive latitudinal distribution, the rock squirrel's altitudinal distribution is difficult to define. It has been reported from near sea level on Tiburon Island, Sonora (Hall, 1981) to 2,900 m in Arizona (Hoffmeister, 1956).

FOSSIL RECORD. Remains of *S. variegatus* are known from a late Rancholabrean (Wisconsinan) and early Holocene site in Arizona (Mead and Phillips, 1981) and from late Rancholabrean sites in California, New Mexico, Texas, and Wyoming (Kurtén and Anderson, 1980). An extinct otospermophile, *S. wilsoni*, from early and middle Pliocene (Clarendonian and Hemphillian) of northern Oregon and southern Washington, may have been ancestral to *S. variegatus* (Black, 1963). Nothing is known of the history of the rock-squirrel lineage between midPliocene and late Pleistocene; this hiatus reflects the difficulty of interpreting the numerous but fragmentary remains of early sciurids (Bryant, 1945; Hazard, 1961; Hibbard, 1941, 1954; Kurtén and Anderson, 1980).

The geographic range of the rock squirrel has changed since the late Pleistocene. Three late Pleistocene records show that the former range was more extensive: the La Brea tar pits (Los Angeles, California); McKittrick tar seeps north of Los Angeles, about 320 km W of the present range; and Little Box Elder Cave west of Douglas, Wyoming, about 200 km N of the current range limit in Colorado (Kurtén and Anderson, 1980). Rock squirrels likely expanded their range in some areas during the so-called climatic optimum at the end of the Pleistocene but contracted it again as climates cooled (Long, 1971). Remains of rock squirrels have been found in four archeological sites in Val Verde Co., Texas. These squirrels probably have been present in Trans-Pecos Texas since late Pleistocene, but their absence from numerous other caves indicates that they moved into central Texas only about 4,000 years ago (Dalquest et al., 1969).

FORM AND FUNCTION. Cuticular scales of the hair of rock squirrels have a mosaic pattern, common in mammals, in which the visible portion of each scale is wider than long (Short, 1978). Dorsal guard hairs of rock squirrels can be distinguished from those of other mammals by a combination of other features (Mayer, 1952): simple form, compound medulla (as in sciurids generally), moderate size (more than 125 μm wide and less than 20 mm long), shaft with alternating bands of pigment (dark tip with distal and proximal light bands separated by a dark band).

Adult rock squirrels molt once a year, usually in midsummer, but later at higher altitudes and latitudes (Bradley, 1929; Davis, 1944; Hall, 1946; Juelson, 1970; Stalheim, 1965). Adult females molt while still lactating and at the same time as adult males (Johnson, 1979; Mearns, 1907). In New Mexico, molt by adults requires 5 to 6 weeks. Molts begin in a band over the neck and continue both cephalad and caudad. A definite molt line is visible as the molt progresses over the anterior part of the body, but on the rump patch several small areas of hair are replaced simultaneously (Stalheim, 1965). There may be individual or populational differences in progression of molt, for Johnson (1979) reported the molt of adult rock squirrels in central Texas to progress toward the head and in a patchy pattern. Young rock squirrels undergo both juvenile and subadult molts (Juelson, 1970).

Squirrels emit a musky scent from anal glands when disturbed (Johnson, 1979). Skin glands that secrete an oily substance with a faint musky odor occur on the dorsum immediately posterior to the shoulders. These glands are used apparently to mark objects (Juelson, 1970).

Female rock squirrels usually have five pairs of mammae, although individuals with four pairs have been reported (Hill, 1942; Mearns, 1907; Moore, 1961). Sexually mature males have large scrota (average diameter 50 mm) covered with black hair, which does not appear until the animal is about a year old (Layton, 1973).

The baculum has the same general form as those of other ground squirrels, with an enlarged, knob-like proximal end, narrow shaft, and a spoon-shaped distal end edged with spines; distally there is a midventral projection (Burt, 1960). The baculum of *S. variegatus* is indistinguishable from that of *S. beecheyi* but differs from that of other ground squirrels in being narrower, especially distally, and in having only a few (2 to 6) spines on each side of the spoon in contrast to four or more (up to 12) in other species (Burt, 1960; Wade and Gilbert, 1940). Burt (1960) reported means and ranges of measurements (in mm) of seven bacula (six of *variegatus* and one of *beecheyi*): length, 4.1 (4.0 to 4.5); width of base, 0.8 (0.6 to 1.1); width of distal end, 0.8 (0.6 to 1.1). The os clitoridis, as depicted and described by Layne (1954:360, Fig. 1) is rodlike, 2.0 mm long, has a dorsal sulcus distally but lacks spines characteristic of other species of ground squirrels. The absence of spines probably was an artifact of the preparation (drying) of Layne's specimen.

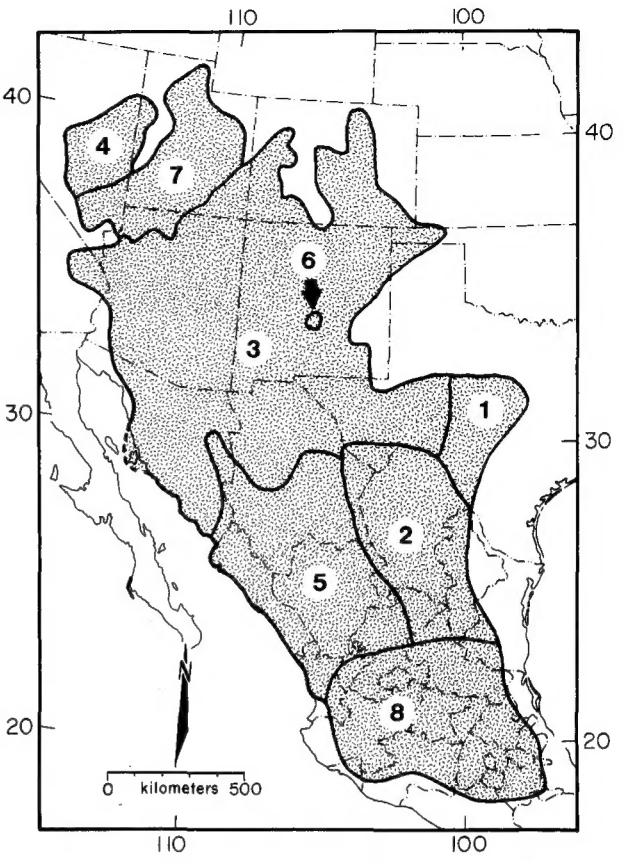

FIG. 4. Distribution of *Spermophilus variegatus*. Subspecies are: 1, *S. v. buckleyi*; 2, *S. v. couchii*; 3, *S. v. grammurus*; 4, *S. v. robustus*; 5, *S. v. rupestris*; 6, *S. v. tularosae*; 7, *S. v. utah*; 8, *S. v. variegatus*. Map redrawn by DFS after Hall (1981).

In many muscular and skeletal characteristics the rock squirrel appears to be intermediate between tree squirrels (for example, *Sciurus*) and more advanced ground squirrels, such as members of the subgenus *Spermophilus* (Bryant, 1945). The extensive descriptions by Bryant (1945) refer to a composite sample of rock squirrels and other members of the subgenus *Otospermophilus* that he used as a standard for comparison of sciurid genera and subgenera. Specific references to the rock squirrel consist of illustrations of the skull (Figs. 7, 21, 35), teeth (Plate 2, Fig. b; Plate 6, Figs. g to h), superficial facial musculature (Figs. 45 to 46), and extrinsic musculature of the cheek pouch (Fig. 47), and ratios between various pairs of skeletal elements (Table 2). Bryant (1945) concluded that body form, dentition, and shape of the skull of *Otospermophilus* retained more primitive characters than that of any other subgenus of *Spermophilus* with the possible exception of *Callospermophilus* (golden-mantled ground squirrels).

Auditory ossicles of the rock squirrel have the general sciurid form (Cockerell et al., 1914). The malleus has a large, high head, angled surface for articulation with the incus, straight neck, and narrow manubrium. The incus is stout and ridged, the stapes large.

Spermophilus variegatus has large internal cheek pouches, approximately 25 mm long and 15 mm high when relaxed but reaching to the sternum when stretched (Bryant, 1945; Juelson, 1970). They open slightly anterior to the cheekteeth. The pouches develop by evagination from the oral cavity into the buccinator muscles and extend posteriad between the sphincter colli and masseter muscles. Extrinsic muscles of the pouch are modified parts of

the facial musculature. A large pit in the ventral surface of the premaxilla immediately behind the incisor marks the attachment of one of these muscles (Bryant, 1945). Intrinsic muscles of the pouches of *S. variegatus* have not been described. Juelson (1970) counted 62 acorns of Gambel's oak (*Quercus gambelii*) averaging 20 by 13 mm carried in the pouches of one squirrel. Other examples illustrating the large capacity of cheek pouches of rock squirrels include: 104 seeds of wild lupine (*Lupinus* sp.) plus parts of others (Cahalane, 1947); 360 *Purshia* seeds in one individual's pouches, in another's 234 pinyon (*Pinus edulis*) nuts (Anderson, 1961); 80 *Ephedra* fruits (Hall, 1946).

Fine structure and location of the hormone-producing cells of the adenohypophysis appear to be similar to those of other mammals (Girod and Dubois, 1976; Girod and Lhéritier, 1981).

The lens of the eye contains a large amount of yellow pigment, which has been suggested to function as a filter for light of high intensity (Dice, 1938).

Squirrels living in areas in which cadmium, copper, selenium, and zinc occur in high concentrations tend to accumulate these trace metals in their tissues (Sharma and Shupe, 1977*a*, 1977*b*).

ONTOGENY AND REPRODUCTION. Males become capable of breeding after emergence from hibernation, rather than emerging in full breeding condition as most other ground squirrels. Females attain the estrous condition about 1 week after males are ready to breed. Testes are scrotal only during the breeding season, at which time they average 32 mm in length; later they average 11 mm (Juelson, 1970). The breeding season lasts about 1 month in northern Utah, peaking in midMarch at altitudes near 1,370 m (Juelson, 1970), and about 6 weeks in March and April in central Texas (Johnson, 1979). Stalheim (1965) observed behavior he interpreted as courtship from April 23 through July 29 in central New Mexico at 1,980 m. Males with scrotal testes were observed by Young (1979) in Kimble Co., Texas from May through August. Late breeding by yearlings may lengthen the reproductive season.

The gestation period is not documented. Dates on which pregnant females have been collected range from late March through July in various parts of the range (Anderson, 1972; Baker, 1956; Bradley, 1929; Davis, 1944, 1960; Holdenried and Morlan, 1956; Hooper, 1941; Juelson, 1970; Mearns, 1907). In a particular region, squirrels breed earlier at lower altitudes than at higher ones (Davis, 1944; Juelson, 1970), at least in part because altitude affects the timing of emergence from hibernation. No latitudinal trend in the timing of reproduction is evident.

Rock squirrels reportedly have two litters per year in some southern regions with short winters (Borell and Bryant, 1942; Bradley, 1929; Dalquest, 1953). However, unequivocal data obtained by following individual females through two successful pregnancies in one season are lacking. Only one litter per season is reported for populations in northern Utah (Juelson, 1970), central Texas (Johnson, 1979), west Texas (Layton, 1973), and central New Mexico (Stalheim, 1965).

Embryo counts range from three to nine with an overall average of approximately five (Anderson, 1972; Baker, 1956; Bradley, 1929; Davis, 1944; Holdenried and Morlan, 1956; Hooper, 1941; Juelson, 1970; Mearns, 1907). Numbers of young emerging from the natal burrow range from one to seven with an average of approximately four (Dalquest, 1953; Davis, 1960; Johnson, 1979; Juelson, 1970; Layton, 1973; Long, 1940). Juelson (1970) estimated that emerged young might represent 75% of embryos implanted. Available data do not indicate geographic trends in litter size.

Rock squirrels are born hairless (except for 2 mm vibrissae), unpigmented, blind, and with closed ears. Four young born in captivity averaged 7.8 g at birth (Juelson, 1970). Neonates can crawl slowly, using primarily the forelegs. They squeak when disturbed. Pigment in the skin is first visible on the third day after birth; hair other than vibrissae appears on the seventh day, and the young are well pigmented and active at this time. On the 10th day, they can hold their heads up easily and can crawl using quadrupedal movements that resemble adult walking. The lower incisors erupt on about the 14th day. By the 17th day, the last day observations were made by Juelson (1970), the young were well haired on dorsal surfaces and well coordinated in movements.

Reported dates of first emergence of young rock squirrels range from the end of May to mid-August (Johnson, 1979; Juelson, 1970; Layton, 1973; Stalheim, 1965). Age at first emergence is estimated to average about 8 weeks (range 6 to 10 weeks) from indirect evidence (Johnson, 1979; Juelson, 1970; Layton, 1973; Stalheim, 1965). Lactation lasts about 2 months (Johnson, 1979). Young begin to forage for themselves on the third day after emergence (Stalheim, 1965). At emergence, young rock squirrels weigh about 100 g (Johnson, 1979; Layton, 1973). One litter captured soon after emergence reached approximately 90% of adult length after about 8 weeks in captivity (Stalheim, 1965). Subsequent growth was much slower, and length did not increase significantly during the next 4 months. Johnson (1979) suggested that young squirrels continue to gain weight for more than 2 years after birth.

ECOLOGY. *Spermophilus variegatus* is primarily a species of the semiarid Upper Sonoran Zone, although it may extend upwards into the Transition Zone and descend into the Lower Sonoran Zone (Bailey, 1932; Baker, 1956). It tends to be absent from open plains, wide valleys, deserts, and the higher montane forests.

As its common name suggests, the rock squirrel is a resident of rocky habitats, and throughout its geographic range the local distribution is dictated by the presence of rocks, stones, and boulders in the form of talus slopes, rocky hillsides, canyons, arroyos, and cliffs (Bailey, 1932; Davis, 1944; Findley et al., 1975; Howell, 1938; Schmidly, 1977). In lieu of natural rocky habitats, rock squirrels exploit man-made structures such as old buildings, bridges, terraced roads, and stone walls (Bailey, 1932; Baker, 1956; Baker and Greer, 1962; Johnson, 1979).

Burrows are located under large rocks, bushes, trees, or other cover with prominent observation points nearby. Rock squirrels also occasionally den in trees (Bailey, 1905). Burrows are shallow (about 0.3 to 1 m) and usually short (to 1.5 m; Juelson, 1970; Layton, 1973), but longer ones, to 5.8 m, have been excavated (Stalheim, 1965). There is one main tunnel, 8 to 30 cm (usually 10 to 12 cm) in diameter, with one to three openings to the outside and a connecting nest chamber (Juelson, 1970; Layton, 1973; Stalheim, 1965). Feces are deposited in a side tunnel near the nest chamber (Juelson, 1970). Burrows are lined with dried grass, leaves, bark, and seed pods (Bradley, 1929; Stalheim, 1965; Steiner, 1975). Adults have a home burrow and auxiliary burrows used while foraging (Juelson, 1970; Young, 1979). Burrows are used year after year (Bailey, 1932), although there appear to be seasonal movements by individual squirrels from one burrow location to another (Layton, 1973). Deserted rock squirrel burrows are used by burrowing owls, *Speotyto cunicularia* (Martin, 1973) and probably by other animals.

Home ranges are large and overlap greatly; the size varies with season and breeding condition of the squirrels (Johnson, 1981; Juelson, 1970; Stalheim, 1965). Males often occupy areas distinct from females, except during the breeding season when the range of a resident male overlaps that of one or more females (Johnson, 1981). In central Texas in spring, means of areas (ranges in parentheses) of home ranges (in ha) were: resident male, 0.40; 11 breeding females, 0.15 (0.12 to 0.22), calculated by minimum polygon method (Johnson, 1981). During times of lactation and emergence of the young (late May–July), breeding females in Johnson's (1981) study became more territorial and excluded the resident male, and the mean size of home ranges shrank to 0.09 ha. Stalheim (1965) reported minimum home ranges (Mohr, 1947) averaged 0.43 ha for females and 0.23 ha for males, based on sightings and captures over a 2-month period during summer. Means of areas (ranges in parentheses) of minimum home ranges (in ha) for squirrels in northern Utah during the latter half of July (Juelson, 1970) were: three adult males, 0.32 (0.23 to 0.45), four adult females, 0.24 (0.11 to 0.30).

The density of a rock-squirrel population in central Texas in spring was 13 squirrels in an area of 1 ha (Johnson, 1981). Densities reported by Juelson (1970) for areas of marginal and good habitat were 2.0/ha and 5.7/ha, respectively. The sex ratio for the species as a whole probably is 1:1, but is modified locally by social structure. Males apparently move considerably during the breeding season; after that time, adult females may move into or out of a colony (Johnson, 1981). Many juveniles disperse from the maternal home range in late summer or early fall; yearlings may leave the parental range in spring (Johnson, 1979). During summer, squirrels tend to stay within 100 m of the home burrow (Juelson, 1970; Layton, 1973). Hooper (1941) found normally colored squirrels living on dark lava beds in New Mexico and concluded that significant movements occurred onto and off the areas of lava, sufficient to prevent selection for a dark population on the lava.

Rock squirrels consume a wide variety of food items, including nuts, seeds, grain, berries, fruit, roots, green vegetation, cactus, invertebrates, and fresh and dried meat (Bailey, 1905; Burt, 1934; Mearns, 1907; Young, 1979). The diet of rock squirrels changes seasonally depending upon local availability with more green material consumed in spring, berries in summer, and seeds, grains, and nuts in autumn (Bailey, 1932). Stalheim (1965) reported that rock squirrels select reproductive rather than vegetative parts of plants. He also noted that although rock squirrels in the Sandia Mountains, New Mexico, consumed a wide variety of plant foods, the following provided the bulk of the diet: berries of wild sumac (*Rhus trilobata*), blossoms and fruit of Apache plume (*Falluquia paradoxa*), heads of assorted grasses, predominantly wild rye (*Elymus* sp.), heads of ragweed (*Ambrosia* sp.), gooseberries (*Ribes* sp.), and acorns (*Quercus turbinella* and *Q. grisea*). Each of these major food items became available progressively during the summer, and rock squirrels shifted their diets accordingly (Stalheim, 1965). Other reports of plants utilitzed in specific areas are available for northern Utah (Juelson, 1970) and west Texas (Layton, 1973). Howell (1938) observed that nuts, including acorns, walnuts (*Juglans* sp.) and pine nuts (*Pinus edulis*) probably compose a large portion of the diet of rock squirrels but also listed seeds of the following plants among its constituents: mesquite (*Prosopis*), cactus (*Opuntia*), saltbush (*Atriplex*), wild gourd (Cucurbitaceae), wild cherries (*Prunus*), fragrant sumac (*Rhus aromatica*), Nevada jointfir (*Ephedra nevadensis*), serviceberry (*Amelanchier*), spurge (*Euphorbia*), marbleseed (*Onosmodium occidentale*), wax currents (*Ribes cereum*), cactus fruit, blossoms of mescalbean (*Sophora secundiflora*), flowers and tips of *Agave*, berries of cherrystone juniper (*Juniperus pachyphloea*), and seed pods of *Yucca* and Indian breadroot (*Psoralea*). Besides feeding on native plants, rock squirrels consume the fruits or seeds of the following domesticated plants: muskmelon, watermelon, apples, cherries, apricots, blackberries, squash, peas, grains, corn, peaches, and pears. As a consequence, rock squirrels have the potential for becoming serious pests in agricultural regions (Howell, 1938). Animal foods eaten by rock squirrels include grasshoppers (Orthoptera; Layton, 1973), beetles (*Lucanus* sp.) and earthworms (Lumbricidae; Bradley, 1929), young wild turkeys (*Meleagris gallopavo*) and domestic fowl (Cook and Henry, 1940), and smaller vertebrates (Layton, 1973). A rock squirrel killed and ate part of a bannertail kangaroo rat (*Dipodomys spectabilis*) in captivity (Cahalane, 1939).

Internal parasites reported from rock squirrels include the protozoans *Babesia wrighti* (Doran, 1954), *Entamoeba citelli, Chilomastix magna, Hexamastix muris, Monocercomonoides pilleata, M. robustus, Octomitus pulcher, Tritrichomonas muris, Sphaerita* sp. (Juelson, 1970); the trematode *Brachylaime microti*, the cestodes *Hymenolepis citelli, Mesocestoides corti*, and *Raillietina retractilis* (Juelson, 1970); the nematodes *Capillaria hepatica, Citellinema bifurcatum, Rictularia coloradensis, Syphacia citelli, Trichuris citelli* (Juelson, 1970) and *Passalurus abditus* and *Trichuris minuta* (Doran, 1955); and the acanthocephalan *Moniliformis clarki* (Juelson, 1970). External parasites include the louse *Neohaematopinus laeviusculus*; larval dipterans belonging to the genera *Hylemya* and *Sarcophaga* and to the families Cecidomyiidae and Phoridae, genera and species undetermined (Juelson, 1970); the mites *Androlaelaps fahrenholzi, Brevisterna utahensis, Hirstionyssus incomptis, Ischyropoda armatus* (Whitaker and Wilson, 1974), *Euschongastia* sp. and *Trombicula* sp. (Juelson, 1970); the ticks *Dermacentor andersoni* (Juelson, 1970), *Ixodes conepati* (Keirans and Clifford, 1974), and *Dermacentor parumapertus* (Layton, 1973); and 19 species of fleas: *Catallagia decipiens, Dactylopsylla* (*Foxella*) *ignota, Diamanus montanus, Echidnophaga gallinacea, Hoplopsyllus anomalus, Monopsyllus wagneri, M. eumolpi, Nosopsyllus fasciatus, Oropsylla idahoensis, Orchopeas sexdentatus, Opisocrotis tuberculatus, Thrassis pandorae, T. acamantis, T. francisi, T. bacchi* (Stark, 1958), *Cediopsylla inaequalis, Hoplopsyllus affinis, Thrassis gladiolis*, and *T. stanfordi* (Juelson, 1970). The rock squirrel is the definitive host for the flea *Hoplopsyllus anomalus* (Stark, 1958). This species and *Diamanus montanus* were the most common fleas on rock squirrels in northern Utah (Juelson, 1970) and New Mexico (Holdenried and Morlan, 1956). Eleven species of fleas reported from rock squirrels, including *D. montanus*, are known or potential vectors of sylvatic plague, and a few instances of rock squirrels infected with this disease have been reported (Allred, 1952; Meyer, 1939; Williams et al., 1978). Rock squirrels are susceptible to the plague organism (*Yersinia pestis*) and apparently serve as a reservoir for this disease (Quan et al., 1985). Some ectoparasites of rock squirrels are known or implicated vectors of tularemia, brucellosis, Q-fever, and Rocky Mountain spotted fever, although the squirrels themselves are not known to be infected with any but the last (Juelson, 1970).

There is little information on longevity or on rates of mortality for rock squirrels. Three marked animals lived at least 29 months during Juelson's (1970) study; they probably were at least 1 year old when marked.

Predators on *S. variegatus* include golden eagles, *Aquila chrysaetos* (Mollhagen et al., 1972; Juelson, 1970) and probably other diurnal raptors; mammalian carnivores such as bobcats, *Lynx rufus* (Jones and Smith, 1979; Juelson, 1970), ringtails, *Bassariscus astutus* (Toweill and Teer, 1977), gray foxes, *Urocyon cinereoargenteus* and raccoons, *Procyon lotor* (Layton, 1973), coyotes, *Canis latrans*, badgers, *Taxidea taxus*, and domestic cats and dogs (Juelson, 1970); rattlesnakes, *Crotalus viridis* (Juelson, 1970) and possibly bullsnakes, *Pituophis melanoleucus* (Haywood and Harris, 1971), and man (Dalquest, 1953; Davis, 1960; Gilmore, 1947) are known to prey on rock squirrels.

BEHAVIOR. Populations of rock squirrels tend to be colonial and are organized as maternal aggregations at prime denning sites with a dominant male and several subordinate males occupying peripheral locations (Johnson, 1979, 1981; Krenz, 1977; Layton, 1973). Dominant males defend a colony from other breeding males but allow females and juveniles to move about freely, and females actively defend, from other adults, the area immediately around the burrow (Johnson, 1981). Both sexes seem to maintain an area of exclusion while foraging (Young, 1979).

Agonistic behavior is highest during the breeding season when males compete for mates (Johnson, 1979). Most fights consist of a flank-to-flank shove followed by a rolling fight (Juelson, 1970; Krenz, 1977); "boxing" also is common (Juelson, 1970). Many adults are scarred on head and flanks from aggressive encounters (Johnson, 1979, 1981; Juelson, 1970; Krenz, 1977).

Courtship is initiated by the male with nasonasal contact, stroking the female's head with its paws, and nasoanal contact. The female may respond by arching her back and raising her tail. Attempts at mounting are resisted and are followed by a chase that usually leads down a burrow (Johnson, 1979; Stalheim, 1965). Copulation has not been observed in the field or laboratory and probably occurs in the burrow.

Females usually remain on the alert while newly-emerged young are above ground; they may move the denning site if disturbed (Johnson, 1979; Young, 1979). Nose-touching by female and young probably effects greeting and recognition. Juveniles appear to recognize siblings; such recognition reduces intrafamilial agonistic behavior, although dominant squirrels displace subordinate siblings from favored perches (Johnson, 1979).

Rock squirrels are diurnal, but timing of peak activity varies seasonally: in fall, winter, and spring the peak is at midday (Johnson, 1979; Juelson, 1970); in summer there may be a single peak in the morning (Johnson, 1979) or afternoon (Young, 1979), or activity in both morning and late afternoon (Bradley, 1929; Juelson, 1970; Stalheim, 1965). Ambient temperature affects activity greatly; squirrels rarely are active below 10°C in northern Utah (Juelson, 1970) or below 15°C in Texas (Johnson, 1979), and usually are not active above 27 to 30°C in northern Utah (Juelson, 1970) and 35°C in Texas (Johnson, 1979). Activity at high temperatures may be restricted to short bouts of foraging in the shade (Layton, 1973; Young, 1979). Light wind may increase activity during hot weather, whereas strong winds inhibit activity (Juelson, 1970) or restrict it to the ground (Young, 1979). Rock squirrels occasionally are active during light rain showers (Johnson, 1979; Young, 1979), but not during heavy downpours (Johnson, 1979; Juelson, 1970).

Rock squirrels communicate mainly by a combination of posture and vocalization (Johnson, 1979; Krenz, 1977). Squirrels familiar with one another usually approach head-on and may make nose contact. Unfamiliar squirrels approach and are approached obliquely and try to assert dominance (Johnson, 1979). Most encounters consist only of threat and counter-threat displays (Krenz, 1977). Vocal communication is used mostly for warning, and among free-living squirrels, only colonial females are reported to call (Krenz, 1977). Five types of calls have been reported: long and short alarm calls, composed of "chucks" and whistles, that serve to locate the

direction of the danger stimulus; whistle alarms, short ventriloquistic whistles given from the burrow; squeals, high-pitched sounds in response to pain or handling; growls, low-pitched noises used during aggressive encounters and when trapped or handled (Krenz, 1977). Rock squirrels also use tooth chattering as a warning or aggressive signal (Johnson, 1979; Krenz, 1977). There is no evidence for a repertoire of calls to distinguish different kinds of predators as reported for some other ground squirrels (Krenz, 1977). Chemical communication may be effected by means of dorsal cutaneous glands; Juelson (1970) observed males to rub their backs on rocks and stems during the breeding season. Squirrels also rub their cheeks against rocks and smell each other's cheeks and around their ears, top of head, back, and anal regions (Johnson, 1979).

Rock squirrels use a slow diagonal walk while foraging and when close to the burrow; distances greater than 1 m are covered usually by running with the bound or half-bound (al-Johny, 1983; Juelson, 1970). Speeds as great as 18 km/h have been recorded in captivity (al-Johny, 1983). In ascending trees and branches, rock squirrels use walking movements and movements that resemble the bound. Squirrels descend head first with the hind feet rotated about 120° to the body axis. The tail is used in balancing and as a prop while sitting on a branch. On small branches, rock squirrels progress cautiously and grasp twigs to maintain balance. Horizontal jumps as great as 165 cm have been recorded; squirrels land on the forefeet first or on all four feet at once (al-Johny, 1983).

King (1965) and King and Goodman (1966) used hand-reared rock squirrels as subjects to compare techniques of measuring learning ability and found these squirrels to be proficient at discrimination and at reversal learning.

Foraging and feeding compose most of the daily activity. Foraging bouts are longest in the morning (average 12 min) and become progressively shorter as ambient temperatures increase during the day (Young, 1979). Rock squirrels forage extensively in trees and on the ground (Juelson, 1970; Krenz, 1977; Mearns, 1907; Steiner, 1975; Young, 1979). Food items often are carried to a lookout point where they are consumed (Juelson, 1970; Young, 1979). Juelson (1970) observed squirrels to bury food in small pits dug outside the burrow, but food caches have not been found within excavated burrows (Layton, 1973; Stalheim, 1965).

Rock squirrels self-groom and dustbathe, possibly in response to the presence of ectoparasites, most often in early morning or late evening (Juelson, 1970; Young, 1979). No true allogrooming has been observed (Johnson, 1979). Rock squirrels sometimes defecate and urinate in small pits in cat-fashion in addition to some use of latrine chambers in the burrow (Johnson, 1979; Juelson, 1970).

All activities are interrupted by short bouts of alert behavior during which the squirrel assumes a half-crouched posture or erect (picket-pin) posture (Johnson, 1979; Juelson, 1970). Squirrels often rest, feed, and sunbathe in trees or on other high lookout points such as rocks or snags, from which alarm calls are easily heard (Bailey, 1932; Burt, 1934; Johnson, 1979; Krenz, 1977; Mearns, 1907; Young, 1979). Offensive behaviors reported include aggressive reactions toward fox squirrels, *Sciurus niger* (Young, 1979) and bullsnakes (Krenz, 1977).

Rock squirrels are shy of being observed, hence difficult to study, both in the wild and in captivity. Trap shyness usually develops after two or three captures (Juelson, 1970), and squirrels avoid burrows with traps near them (Young, 1979). Long-term movements are difficult to measure because of trap shyness.

Spermophilus variegatus is a facultative hibernator, with a circannual rhythm of winter torpor (Pengelley and Kelly, 1966). Rock squirrels store fat for hibernation; adults in northern Utah gained an average of approximately 200 gm between March and September (Juelson, 1970). Squirrels also may store food for winter use (Davis, 1960; Johnson, 1979), although not all do so, and none has been observed to store food in captivity (Pengelley, 1964).

Rock squirrels hibernate throughout much of their geographic range, but the duration of hibernation appears to vary with latitude, altitude, and severity of the winter. Reported dates of emergence and disappearance from the field vary tremendously, and animals may be seen intermittently all winter, especially in mild weather, in most parts of their range (Bailey, 1905; Davis, 1960; Dice, 1938; Krenz, 1977; Long, 1940; Mearns, 1907; Young, 1979). In northern Utah, rock squirrels may hibernate for 1 to 6 months (Juelson, 1970). In Texas, they hibernate 2 to 4 months (November–February or March; Johnson, 1979; Layton, 1973). Adults enter hibernation earlier in the season than juveniles (Juelson, 1970). In west Texas, animals that did not become obese (both adults and young) were active in winter (19 November–15 March), whereas obese individuals were not trappable during that time (Layton, 1973). Adult females begin to store fat sooner and hibernate earlier than adult males (Juelson, 1970), in contrast to the usual pattern in ground squirrels in which males enter hibernation first (Michener, 1984). Young female and young male rock squirrels enter hibernation at the same time. Emergence is not related to age, but females emerge about 1 week before males (Juelson, 1970), again in contrast to the pattern recorded for most ground squirrels.

Rock squirrels may estivate (Juelson, 1970) but apparently not in response to lack of water. They are remarkably tolerant of water deprivation, for individuals have survived up to 100 days on dry food alone with no drop in body temperature (Pengelley, 1964). Captive squirrels from Nevada did not hibernate in October at a low ambient temperature (3°C) when supplied with food, but hibernated when food was removed (Pengelley, 1964). During torpor, rock squirrels maintain a body temperature of 5.5 to 10°C even when ambient temperature is 3°C or lower (Juelson, 1970; Pengelley, 1964). Torpid squirrels undergo periodic arousals and are active for a few hours to 2 days between bouts of torpor. Arousal takes 1.5 to 3.0 h (Juelson, 1970).

GENETICS. *Spermophilus variegatus* has a diploid number of 38 and a fundamental number of 72. There are 22 metacentric and 14 submetacentric autosomes; the X is metacentric and the Y acrocentric. There are no observable karyotypic differences from *S. beecheyi* (Nadler, 1966). Other species of *Spermophilus*, including *S.* (*Otospermophilus*) *adocetus*, differ from these two (Birney and Genoways, 1973; Nadler, 1966).

The genus *Spermophilus* first appears in deposits of mid-Miocene age, and most Tertiary specimens have been assigned to the subgenus *Otospermophilus* by Black (1963), who considered *Otospermophilus* to be an early, generalized ground-squirrel lineage that gave rise to the other living subgenera. Immunological comparisons of *S. variegatus* with *S.* (*Callospermophilus*) *lateralis*, *S.* (*Spermophilus*) *richardsonii*, and *S.* (*Ictidomys*) *tridecemlineatus* indicate that *S. lateralis* is closest of these to the rock squirrel, although still a considerable distance from it (Gerber and Birney, 1968). Likewise, Hafner (1984:13, Fig. 1.3) indicated that the subgenera *Callospermophilus* and *Otospermophilus* are closer genetically to each other than either is to any other subgenus in *Spermophilus*. This relationship had been suggested earlier on morphological grounds by Bryant (1945), although Black (1963) placed *S. lateralis* farther from the Recent rock-squirrel lineage. Of living otospermophilines, *S. beecheyi* is closest to *S. variegatus* in many features. However, Black (1963:237, Fig. 8) showed these two species were separate since the early Pliocene, suggesting a long period of evolution of *S. variegatus* independent from other living members of the genus *Spermophilus*.

Populations of rock squirrels in New Mexico and Colorado exhibit polymorphism in serum proteins; two or three separate albumin fractions are present in individual squirrels, and significant variation in concentration and relative mobilities of transferrins exists (Seaman and Nash, 1977).

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